OBSERVATIONS ON THE SUBAERIAL DIATOM *NAVICULA SPINIFERA* BOCK, AND ITS TRANSFER TO *LUTICOLA* MANN

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ABSTRACT — *Navicula spinifera* Bock, a little-known subaerial diatom reported only once in the literature so far, was studied from material collected at several sites in Turkey. Its morphology was examined with the light and scanning electron microscope, enabling an assessment of its taxonomic position within the classification proposed by Round *et al.* (1990) for the Naviculales. The extension of the plastid beneath both valve faces, the presence of a stigma and a longitudinal canal, of which the inner wall is developed into an arched flap-like structure at the opposite side of the stigma, as well as the dentate valvocopulae, allow the species to be accomodated within *Luticola*, rather than within *Diadesmis*. Yet, it presents certain features which affiliate it with the latter genus as well (e.g. elongated poroids, linking spines, absence of notches on the mantle edge, simplicity of the raphe). The transfer of *Navicula spinifera* to *Luticola* is proposed, after examining the specific characters of this genus. It is suggested that the formation of band-like colonies, such as displayed by this species, may be advantageous for small-sized subaerial diatoms exhibiting a saxicolous microhabitat specialization. In addition, the new combination *Luticola nivaloides* (Bock) Denys & De Smet is proposed for *Navicula nivaloides* Bock.

RESUMÉ — *Navicula spinifera* Bock, une diatomée subaérienne assez mal connue, a été étudiée à partir de récoltes effectuées dans plusieurs sites de Turquie. L'examen de sa morphologie en microscopie photonique et au microscope électronique à balayage a permis de déterminer sa position taxinomique dans la classification proposée par Round *et al.* (1990) pour les Naviculales. Le développement du chloroplaste sous les deux valves, la présence d'un stigma et d'un canal longitudinal dont la paroi intérieure forme un relèvement en arc du côté opposé au stigma, ainsi que les valvocopulae dentées, indiquent que cette espèce serait mieux placée dans le genre *Luticola* que dans le genre *Diadesmis*. L'espèce présente néanmoins certaines caractéristiques qui la rapprocheraient de ce dernier genre (par exemple, poroïdes alongés, épines de jonction, absence d'encoches au bord inférieur du manteau, raphé très simple). Le transfert de *Navicula spinifera* dans le genre *Luticola* est proposé, après examen et discussion des critères qui permettent de définir ce genre. L'hypothèse est proposée que la formation de colonies en bandes, comme observé chez l'espèce étudiée, est favorable à des diatomées subaériennes de petite taille, adaptées à une vie saxicole. En outre, la nouvelle combinaison *Luticola nivaloides* (Bock) Denys & De Smet est proposée pour *Navicula nivaloides* Bock.

KEY WORDS — Bacillariophyceae, *Navicula spinifera*, *Navicula nivaloides*, *Luticola*, *Diadesmis*, saxicolous diatoms, morphology, ultrastructure, colonial growth, Turkey.

INTRODUCTION

Since its description by Bock (1970), no further records of the subaerial diatom *Navicula spinifera* seem to have appeared in the literature. So far the species has only been recorded from wall joints at two sites: San Gimignano (Italy) and Bodiam Castle, Sussex (South England; not mentioned by Hartley, 1986). To some extent this comes as a surprise since it is quite characteristic and easily recognized. The row of large spines ornamenting the valve margin, from which the species lends its name, and its tendency to form short ribbon-like colonies are certainly some of its more prominent features, shared with only few others in the genus *Navicula* Bory in its 'classic' conglomerate sense (e.g. Hustedt, 1961-1966). With the epithet *Navicula* now being reserved for the group of taxa morphologically similar to the *typus generis N. tripunctata* (O.F. Müller) Bory (Cox, 1979), most of the ribbon-forming species, with or without marginal spines, have been placed in the resurrected genus *Diadesmis* Kützing (Round *et al.*, 1990). Occasionally, marginal spines may also be present in members of *Luticola* Mann *in* Round *et al.*, the second genus within the *Diadesmidaceae* Mann *in* Round *et al.*, comprising the group of taxa allied to *Navicula mutica* Kützing (Round *et al.*, 1990) and including the stigma-bearing species of *Navicula* subg. *Punctulata* (Grun.) Patr. Such is the case in *L. lagerheimii* (Cleve) Mann *in* Round *et al.*, a South-American species, which also grows in band-like colonies, like most *Diadesmis* spp. Both *Diadesmis* and *Luticola* are especially common in subaerial habitats.

The taxonomic position of *Navicula spinifera* has remained undetermined so far. Krammer & Lange-Bertalot (1986) acknowledge that the presence of an isolated stigma in the central area of the valve points to a relation with the *N. mutica* group, but that its tendency to form (short) chains and the presence of linking spines are features shared with *Diadesmis gallica* W. Smith. This uncertainty is also reflected by the fact that, unlike very few other species in the vicinity of *N. mutica* or *D. gallica*, *N. spinifera* was not reallocated by Mann (Round *et al.*, 1990).

In view of the problems associated with the revision of *Navicula s.l.* (see e.g. Reichardt, 1992; Lange-Bertalot & Moser, 1994) a closer examination of the 'left-over species' in this group is not without importance. Although Round *et al.* (1990, p. 532) state in their discussion of *Luticola* that "There is little risk of confusing with any other genus ...", and Krammer & Lange-Bertalot (1986) do not disfavour the separation of the *Navicula mutica* group as a separate genus, Lange-Bertalot's (1993, p. 89) comment "Die Definitionen, verbunden mit den Zuordnungen von Taxa zu den Gattungen *Luticola*, ... können (vorläufig?) noch überhaupt nicht überzeugen." clearly indicates the need for further study in this respect.

The occurrence of *Navicula spinifera* in some samples collected by the first author to study subaerial diatom assemblages of West-Turkey and Anatolia, allowed a more detailed appreciation of the frustule morphology of this species, using both light microscopy (LM) and scanning electron microscopy (SEM), as well as some observations on the plastid in intact cells. The results and their bearing on the position of the species and the generic characters of *Diadesmis* and *Luticola* are discussed in this paper. Additionally, the taxonomic status of *Navicula nivaloides* Bock is reconsidered, based on the investigation of Turkish material.

MATERIAL AND METHODS

Navicula spinifera was found in the following samples (percentages are based on counts of at least 500 valves; + indicates presence outside the count):

1. Ürgup, 23-4-1987; scrapings from moist piece of calcareous volcanic tuff, scantely grown with liverworts, on the floor of a small cave used as a water reservoir; some 2 m from the entrance and shaded; *Navicula spinifera* 3.3 %, *Diadesmis gallica* 30.9 %, *D. contenta* (Grun.) Mann 22.4 %, *Denticula subtilis* Grun. 19 %, *Amphora normannii* Rabenh. 17.5 %.

2. Ürgup, 28-4-1987; rather dry mosses (*Tortella* sp.) on calcareous volcanic tuff rock overhanging a dried-up water reservoir; shaded; *Navicula spinifera* 70.9 %, *Luticola mutica* (Kütz.) Mann *in* Round *et al.* 18.7 %.

3. Ortahisar, 24-4-1987; scrapings from seepage track on rock wall of calcareous volcanic tuff; *Navicula spinifera* 0.2 %, *Amphora veneta* Kütz. 73.1 %, *Nitzschia hantzschiana* Rabenh. 6.9 %.

4. Kekova Island, 4-5-1987; rather dry mosses (*Tortella* sp.) on lime-stone wall of vaulted passage; shaded; *Navicula spinifera* 0.2 %, *Navicula nivaloides* Bock 33.6 % (see appendix), *Diadesmis contenta* 31.2 %, *Hantzschia amphioxys* 22.4 %.

5. Dalyan, 7-5-1987; slightly damp mosses (*Tortella* sp.), moistened by some dripping water from time to time, on wall of Lycian tomb excavated in lime-stone rock; shaded; *Navicula spinifera* 0.4 %, *Nitzschia hierosolymitana* Mann 67 %, *Hantzschia subrupestris* Lange-Bertalot 18.4 %.

6. as No. 3; rather moist mosses (*Fissidens* sp.) on weathered floor of the burial chamber, wetted by water dripping from the ceiling; shaded; *Navicula spinifera* 5.6 %, *Nitzschia hierosolymitana* 52.8 %, *Navicula nivaloides* 8 %, *Luticola nivalis* (Ehrenb.) Mann *in* Round *et al.* 7.6 %.

7. Ephesos, 10-5-1987; rather dry mosses (*Tortella* sp.) on calcareous sand-stone wall of vault in the "Bath of the Drunks"; shaded; *Navicula spinifera* +, *Diadesmis contenta* 98 %.

The samples were cleaned by adding H_2O_2 and heating to 80 °C for about 1 h, whereafter the reaction was completed by addition of $KMnO_4$. Carbonates were removed with 1 N HCl. Solutes were removed by washing with distilled water and subsequent settling in test tubes. Cleaned material was mounted in Naphrax and observed with a Leitz Orthoplan microscope (DIC optics). Fresh material was suspended in water to examine shape and position of the plastid. For SEM, some suspension of cleaned material was filtered over Milipore RA 1.2 μm and pieces of filter were mounted on aluminium stubs, air-dried and gold-coated. A Philips SEM 515 was used, operated at 20 kV. Most observations were made on sample No. 2 from Ürgup, which yielded the highest concentration of frustules. Splits from samples 2 and 4 were deposited in the collection of the Nationale Plantentuin van België, Meise (BR).

RESULTS

Frustule morphology.

The cells observed in the LM largely fit the description given by Bock (1970; and repeated in Krammer & Lange-Bertalot, 1986). In girdle view (Figs 1-5), the heavily silicified cells are rectangular to square, with rounded corners, giving them a barrel-like appearance. As the pervalvar height of entire cells often exceeds their width, girdle views occur more commonly than valve views. The pervalvar height of single cells was measured to vary between 5.4 and 14 µm; their length ranged from 8.1 to 14.6 µm (9-15 according to Bock, 1970). Often the edges of some of the copulae can be observed. With a length of 0.5 to 2.5 µm (if not worn), the conical marginal spines are quite obvious (Figs 1-2). They are situated at the junction of valve face and mantle, and directed somewhat outward from the pervalvar axis. They are sharply pointed and ca. 0.5 µm thick at their base. Their distance from each other is rather irregular, with a density amounting to 6-10 in 10 µm. Unlike in *Diadesmis gallica* or *D. brekkaensis* (Petersen) Mann, they are always present. A single row of coarse elongated poroids, about 14 to 18 in 10 µm, is present on the rather narrow mantle, somewhat below the spines (Figs 2-3).

The valve face is broadly elliptic to rhombic with obtuse ends (Figs 6-15). The width varies between 5.9 and 9.7 µm (7 to 9 in Bock, *loc.cit.*). The filiform raphe is situated in the middle of the valve. It is straight or slightly curved. The terminal ends are inconspicuous and without terminal fissures (Figs 6, 9). The proximal endings are rather distant and appear as very small roundish pores (Figs 6, 9).

In general, the valve has two rows of rounded to more or less elongated poroids on both sides of the raphe, forming radiate striae with a density of 20 to 24 in 10 µm, measured along the raphe (which agrees with Bock's drawings — the number of only 15-18 striae per 10 µm indicated by this author refers to measurements at the margin of the valve). The outer row follows the circumference of the valve. Its poroids are more strongly elongate, except in the part between the central raphe endings, where they rapidly become shorter, leaving a broad more or less rectangular to oval central area. The inner row of smaller poroids is situated close and ± parallel to the raphe, sometimes slightly bending outward shortly before the central raphe endings, between which it is always interrupted. Accordingly, the axial area is narrow and linear or slightly widened towards the middle. Some isolated poroids or a third row of them may occur between the inner and outer rows. If present, this row is often reduced to the more distal parts (Fig. 26). The poroids, especially those of the outermost row, are commonly placed rather irregularly and of different length, resulting in a wavy disposition of the valve ornamentation.

Usually, the central area presents a number of vague markings of indistinct nature (Bock's "Strukturrudimente"). An isolated stigma is present in the part of the central area from which the central raphe endings are turned away, about halfway between raphe and valve margin. The appearance of the stigma varies with focussing, becoming more square to slightly elongate at high focus and more or less round at low focus.

At low focus, the spines at the valve margin show up as black dots. Due to the gentle slope of the mantle, its row of poroids can be detected near the valve rim, even when the valve is not tilted.

With the SEM, the cingulum can be seen to consist of up to eight open bands with well developed ligulae (Figs 16-19). The valvocopula fits to the mantle with a stepped suture, and posesses coarse tooth-like projections, which extend over the transapical costae on the mantle interior (Figs 20-21). Contrary to *Diadesmis*, *Luticola* species are known to have dentate valvocopulae (Round *et al.*, 1990). In both genera, the copulae usually have one or two rows of perforations. These may be small round pores or, in the case of *Diadesmis*, more slit-shaped as well (Rosowski, 1980; Phipps & Rosowski, 1983; Mayama & Kobayasi, 1986; Round *et al.*, 1990; Albertano *et al.*, 1995). In spite of an intensive search, we were unable to find any trace of perforations on the exterior part of the cingular bands in *Navicula spinifera*. Two rows of very fine grooves or pits could be observed on the inside of the valvocopulae only (Figs 21-22).

The mantle presents no special features apart from the row of large poroids. Its edge is smooth; small notches, such as those occurring in *Luticola* spp. (Round *et al.*, 1990), are absent. The upper part of the mantle and the valve face are in an obtuse angle to each other.

The adherence of cells to each other is maintained by the valve faces and the interdigitating linking spines of variable length (Fig. 19). The latter may be lodged firmly against the mantle of the sibling cell, or their slight curvature may allow them to be hooked into each other (Figs 23-24). The spines are thorn-shaped and are not flattened or spatulate such as in *Diadesmis gallica* (see Lange-Bertalot, 1980; St. Clair *et al.*, 1981; Round *et al.*, 1990; Albertano *et al.*, 1995). Sometimes two spines are joined to each other at their base (Figs 18, 23-24).

The external valve faces of different cells show considerable variation in the position, presence and size of structural elements. Whereas some have an essentially smooth surface, with only some minor irregularly formed or wart-like silica deposits in the central area (Fig. 25), the valve faces of others are roughened by more extensive outgrowths both in the centre and between the poroids, where they may even form longitudinal ridges (Figs 26-27). Near the proximal raphe endings, one or two horn-like projections of almost up to 1 µm long may emerge. This marked surface texture may provide additional adherence for neighbouring cells. Their lesser development or absence in some valves does not appear to result from erosion. Beside the proximal raphe endings and in the central area small pit-like depressions may be present, which do not penetrate the wall completely (Figs 25-26). Sometimes these may extend to the closest poroids, or even along most of the raphe (Fig. 28). Rather similar structures are found with *Diadesmis gallica* and *D. contenta*, but here their shape and placement is more regular (Krammer & Lange-Bertalot, 1986; Round *et al.*, 1990). *Luticola goeppertiana* (Bleisch) Mann *in* Round *et al.* presents a row of rounded pits at the edge of the central area opposite from the stigma (Mayama & Kobayasi, 1986).

The raphe slit is bordered by thin siliceous ridges (Figs 25-27). Externally, the terminal and proximal ends of the raphe are slightly dilated to very small drop-shaped pores of similar shape, the former keeping some distance from the edge of the valve. The central raphe ends are slightly bent away from the stigma. A similarly simple structure is found in some *Diadesmis* spp. as well, although others present T-shaped raphe endings. In *Luticola*, they are generally more extensive and fissure-like (e.g. Lange-Bertalot & Bonik, 1978). Occasionally, the raphe may be reduced to some extent (Fig. 27), although none of the specimens we observed was completely devoid of a raphe, as can happen in certain *Diadesmis* spp. The external opening of the stigma is elongate (Figs 25, 27-28). Compared to the remaining poroids, the openings of those in the middle of the outer row are very small and always round (Figs 25-26). The poroids on the rather gently sloping mantle are aligned with those on the valve face.

This is even clearer when the valve is viewed from the interior, where the alignment of the corresponding elongate alveoli becomes visible (Fig. 29). In intact valves the alveoli of the valve face, each receiving the poroids of a single striae, and those of the mantle are separated by a narrow ridge (Fig. 30). When this is eroded away, the underlying longitudinal canal, formed by a fairly broad interruption of the transapical costae, becomes visible (Fig. 29). The transapical costae (interstriae in the terminology of Mayama & Kobayasi, 1986) are only slightly thickened at the low linking bars and carry no struts. On the side of the valve opposite the stigma, the slope of the transapical costae is distinctly stepped about halfway up. In the middle of the valve and opposite from the stigma, the inner wall of the longitudinal canal is developed into a rather narrow arched siliceous flap, with an entire concave margin (Figs 29-31), similar in shape to that of *Luticola mutica* (see Cox, 1977, pl. 1, fig. 4). The interior opening of the stigma consists of a very small rounded pore situated at the same place as the external slit (Figs 29-30). With the exception of a very slim circular rim around the pore, there are no special structures such as have been documented for several species of *Luticola* (Lange-Bertalot & Bonik. 1978; Mayama & Kobayasi, 1986; Round *et al.*, 1990). The internal opening of the raphe is a mere straight slit, which is broader than the exterior one. The proximal ends may be deflected towards the stigma-bearing side of the valve (Fig. 29), i.e. in a direction opposite to that on the outer valve face. There is no helictoglossa. In the centre, the wall is thickened to a broadly rectangular stauros (Fig. 30).

Life form and cell contents.

The cells are solitary or remain in short chains, usually of only 2-3 (Figs 3-5, 18), but occasionally up to 6 cells long (Fig. 19). They appear to be capable of rather strong adhesion to soil matter.

Each cell contains one plastid with a central pyrenoid lying against one side of the girdle and extending beneath both valve faces with large entire lobes (Figs 32-33). In a fully expanded plastid, these lobes may extend below almost the entire valve face. According to Round *et al.* (1990) this type of plastid is the more common in *Luticola*, whereas in *Diadesmis* it extends only below one of the valves in most cases. However, there appears to be no longitudinal indentation of the lobes beneath the raphe as mentioned by these authors for *Luticola*. The cells may contain several highly refractive spherical bodies, which can be quite large, and presumably represent oil droplets.

DISCUSSION

With exception of the apparently incompletely perforated copulae, the characters of *Navicula spinifera* fit well with those mentioned for the Diadesmidaceae by Round *et al.* (1990). The observations concerning plastid type, presence of a stigma, longitudinal canal and dentate valvocopulae all indicate that *N. spinifera* should be transferred to *Luticola*. Frustular features may be more important than plastid type in this respect, since the plastid may occasionally extend below both valves in *Diadesmis* as well (Round *et al.*, 1990). Moreover, the flap-like structure on the inside of the valve opposite the stigma is restricted exclusively to *Luticola*; the significance of its shape as a species character certainly deserves more attention. The obtuse angle between mantle and valve face seen in this species, and the prominent central pyrenoid (D. G. Mann, 1995, pers. comm.) are other features that suggest a link with *Luticola*, not *Diadesmis*. We therefore propose the following combination:

Luticola spinifera (Bock) Denys & De Smet, *comb. nov.*
Basionym: *Navicula spinifera* Bock 1970. *Nova Hedwigia Beih.* 31, p. 426-427, pl. 1, fig. 12-14, pl. 2, figs 36-37.

Besides the linking spines and the tendency to form bands, several other features are reminiscent of *Diadesmis*: the extremely simple raphe structure, the more distinctly elongate shape of the poroids (especially on the mantle), the relatively large number of copulae, absence of longitudinal indentations in the chloroplast beneath the raphe, and the lack of notches on the edge of the mantle. In part these may represent loss or reduction of features present in other *Luticola* species, and may have developed as convergent adaptations to more extreme environmental conditions. Also, it should be recognized that habitat isolation may be considerable in certain subaerial environments, enhancing diatom speciation (see Johansen & Rushforth, 1994). The intrageneric variability of these characters should, nevertheless, be accounted for in the delimitation of *Luticola*. This study indicates that certain plastid and alveolar features, the structure of the valvocopula, presence of a longitudinal canal and a related flap-like structure, as well as of a stigma, can be considered, presumably, as the more distinctive diagnostic criteria for this group. In our opinion *Luticola* — which even in the LM presents a fairly homogeneous general aspect — is sufficiently different from other *Navicula sensu lato* to merit consideration as a separate and practicable taxonomic unit. A more comprehensive revision of the members of *Luticola* might, however, contribute further to the question which set of characters defines this genus best.

As a "simplified" *Luticola*, the species studied here can be considered as morphologically transitional between this genus and *Diadesmis*. The latter essentially occupies subaerial habitats (e.g. Krammer & Lange-Bertalot, 1986; Round *et al.*, 1990) — although there is at least one record of what appears to be a *Diadesmis* sp. from the marine sublittoral (Navarro, 1982; according to D. G. Mann, pers. comm. 1995, its identity with *D. contenta* is doubtful) — whereas members of *Luticola* have a wider distribution, including various brackish and fresh waters as well. Up to now, *L. spinifera* was exclusively encountered as a saxicolous species, and it may be no coincidence that it shares the ability to form small colonies with *Diadesmis* spp., specialized to withstand the more extreme conditions of life in arid environments. A small cell size can be considered advantageous in this habitat (Bristol, 1920; Lund, 1946), and intraspecific size reduction with increasing drought stress is a well-known phenomenon in diatoms (e.g. Beger, 1927; Lund, 1945; Bock, 1963). Colony formation might offer some compensation for certain less positive consequences of a small size, such as enhanced displacement from the growing site to less suited microhabitats by water or wind (see below) or stronger grazing. Moreover, it will significantly reduce the surface from which water may be readily lost, especially if the girdle elements provide in a prolonged additional sealing of the contact area between cells, such as observed in *Luticola spinifera*. Filamentous growth is also observed in representatives of other diatom genera occurring in lithophytic vegetations such as *Achnanthes* Bory, *Melosira* C. Ag. and *Orthoseira* Thwaites.

Although a biraphid species, the valve structure (*viz.* spines and outgrowths of the valve face) and colonial habit of *L. spinifera* must limit its ability for autonomous movement considerably (*cf.* the tendency towards raphe reduction, also seen in *Diadesmis*). This will reduce its competitiveness in a soil environment, where mobility is required to provide and maintain optimal ambient conditions with regards to moisture, light and nutrients (see Lund, 1945; Brendemühl, 1949; Bock, 1963). This may explain why this diatom appears to occur preferentially on sheltered, more strongly inclined rock surfaces colonized by mosses and in comparable microhabitats with only very shallow soil development.

With regard to its ecology, it may be significant that *L. spinifera* was always found on calcareous substrates. Also, it may be one of the relatively few continental diatoms with a more restricted geographical distribution, *i.e.* centred around the Mediterranean (see Bock, 1970). Our observations from Turkey suggest that it may be less uncommon in suitable habitats throughout this region than supposed previously.

APPENDIX

As mentioned in the introduction, Mann (*in* Round *et al.*, 1990) has already transferred nearly all of the species in the *Navicula mutica* group to *Luticola*. Besides *L. spinifera*, this was, however, also not the case for *Navicula nivaloides* Bock, another subaerial diatom (Bock, 1963; see also Germain, 1981 and Krammer & Lange-Bertalot, 1986). In the LM (Figs 34-35, 37) this species mainly differs from *Luticola nivalis* (Fig. 36) — the most resembling species (it is distinctly different from *Navicula pseudonivalis* Bock both in outline and structure) — by having no more than three rows of areolae, of which the marginal ones appear elongated and distinctly spaced from the single row next to the raphe. Overall, the ornamentation of the valve face of *N. nivaloides* as apparent in the LM is somewhat similar to that of *L. spinifera*. SEM observations (Figs 38-41) show a number of typical *Luticola* features. These include the presence of a stigma with internal cover (Figs 38-39), a stauros-like central nodule (Figs 39-40), and a longitudinal canal (Fig. 41). The flap-like structure is reduced here to a narrow undulating rim (Fig. 40). Externally, the central raphe endings are curved away from the stigma, whereas the hooked polar fissures are fairly large and terminate on the mantle. The helictoglossae are rather well-developed (Fig. 39). The mantle bears a single row of round poroids (Figs 38, 40). The poroids on the valve face are small and more or less round (Fig. 38); the more elongate appearance of the markings in the LM results from the alveolar structure. As in *L. spinifera*, there appear to be no notches at the mantle edge (Figs 39-40). In view of these observations *Navicula nivaloides* should be recombined as well.

Luticola nivaloides (Bock) Denys & De Smet *comb. nov.*
Basionym: *Navicula nivaloides* Bock 1963, *Nova Hedwigia* 5: 236-237, pl. 2, figs 142-149.

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LEGENDS TO FIGURES

Figs 1-15. *Navicula spinifera* in the LM (Turkey, different localities). Fig. 1. Girdle view of valve with copulae, focused on the spines. Fig. 2. Girdle view of complete cell, focused on mantle areolae. Figs 3-5. Colonies of a few cells Note how cells also remain linked to each other by the girdle elements. Figs 6-15. Valve views showing variation in form, size and structure (Figs 8 and 9 are the same valve at high and low focus respectively). Fig. 16. *Navicula spinifera* in the SEM (Turkey, sample 2). Girdle view of dividing cell. Scale bars = 10 µm.

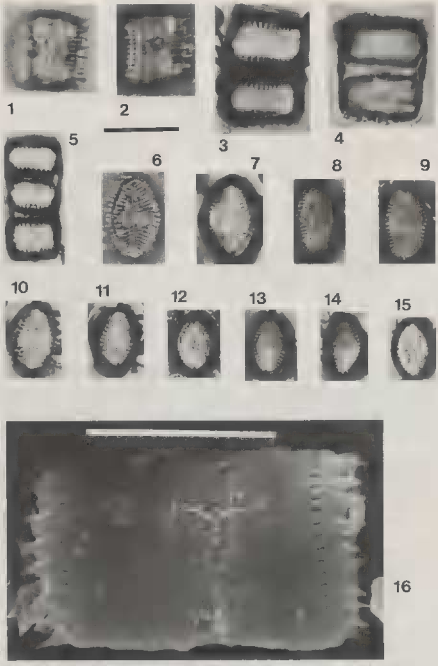
Figs 17-20. *Navicula spinifera* (SEM). Ürgup, sample 2. Fig. 17. Girdle view of cell showing alternating copulae with large ligulae. Figs 18-19. Chains of 3 and 6 cells respectively. Scale bars = 10 µm. Fig. 20. Frustule with one of the valves detached (background), showing dentate valvocopula. Scale bar = 1 µm.

Figs 21-25. *Navicula spinifera* (SEM). Ürgup, sample 2. Figs 21-22. Interior views of valvocopulae, showing double rows of what appear to be only pits or grooves. Figs 23-24. Details of interdigitating linking spines. Scale bars = 1 µm. Fig. 25. Valve face of the "smooth" type. Note the elongate outer opening of the stigma, the circular poroids bordering the central area, depressions along the proximal raphe ends, and small terminal pores of the raphe. Scale bar = 10 µm.

Figs 26-28. *Navicula spinifera* (SEM). Ürgup, sample 2. Valve faces of the "rough" type. Note the large horn-like central extensions on fig. 26, the reduced and partly deformed raphe on fig. 27, and the extensive depressions along the raphe in fig. 28. Scale bars = 1 µm.

Figs 29-31. *Navicula spinifera* (SEM). Ürgup, sample 2. Internal views of the valve. Fig. 29. General view showing the simply structured raphe and round stigma, alveoli and exposed longitudinal canal interrupting the transapical costae. Fig. 30. Oblique view showing stauros and the ridge covering the longitudinal canal (arrow). Fig. 31. Detail of the central part showing the arched flap-like structure (arrow), and the teeth of the valvocopula extending over the transapical ribs. Scale bars = 1 µm. Figs 32-33. *Navicula spinifera* cells with plastids in valve and girdle view respectively (drawn from the LM). Figs 34-35, 37. *Navicula nivaloides* Bock from Kekova Island, sample 4 (LM). Fig. 36. *Luticola nivalis* (Ehrenb.) Mann *in* Round *et al.* from Dalyan, sample 6, in comparison (LM). Scale bars = 10 µm (vertical for figs 36-37).

Figs 38-41. *Navicula nivaloides* from Kekova Island, sample 4 (SEM). Fig. 38. Oblique external view of a frustule. Figs 39-40. Oblique internal views showing stauros, helictoglossae, covered stigma (39, arrow), narrow undulated flap (40, arrow) and entire mantle margins. Fig. 41. Internal view showing demarcation of the longitidinal canal (arrow). Scale bars = 10 µm.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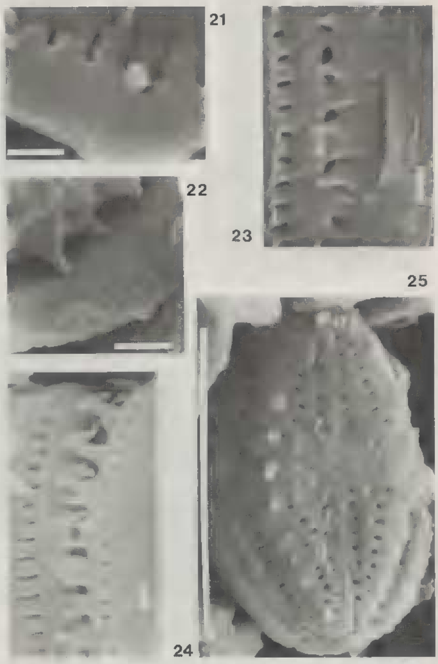
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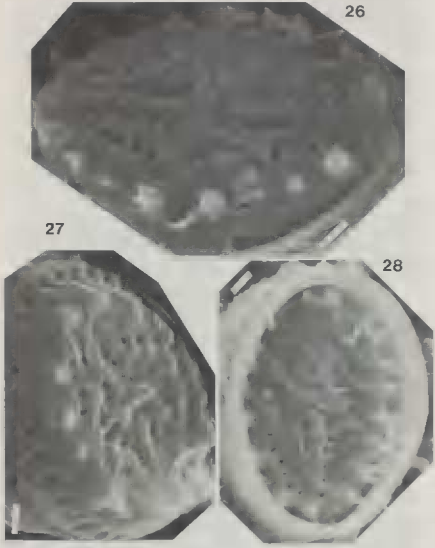
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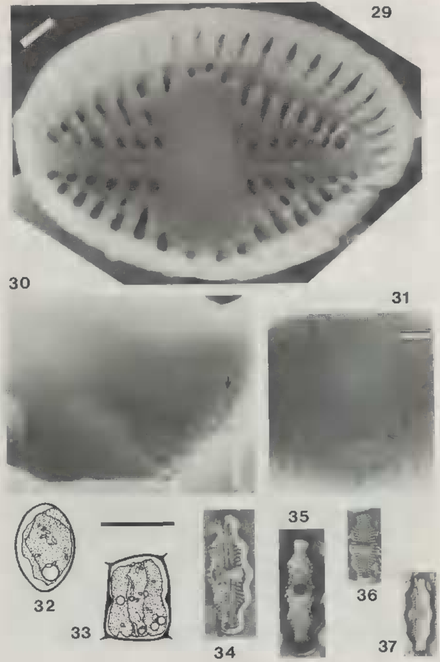
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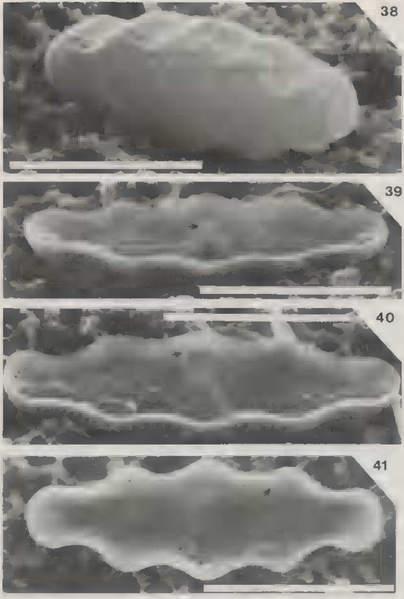
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